

The juvenile stages of eight swimming crab species (Crustacea: Brachyura: Portunidae); a comparative study

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Introduction

The comparative larval morphology of many brachyuran crabs occurring in N Atlantic waters has become better known during the last two decades (see Rice, 1980 for references). However, except for the studies by Lebour (1928), early post-larval stages have not been investigated comparatively to facilitate identifications of young crabs that frequently occur in intertidal and benthic samples. The availability of reared material together with recent rich hauls of juvenile crabs obtained from the Porcupine Sea Bight has prompted this comparative study of the early crab stages of eight swimming crab species all belonging to the family Portunidae and to the sub-family Polybiinae.

Crabs described here are: (1) *Liocarcinus arcuatus* (Leach); (2) *L. pusillus* (Leach); (3) *L. depurator* (Linnaeus); (4) *L. puber* (Linnaeus); (5) *L. holsatus* (Fabricius); (6) *Macropipus tuberculatus* (Roux); (7) *Bathynectes longipes* (Risso); (8) *Polybius henslowii* Leach.

The crab stages (1)–(5) are figured chiefly from material reared in the larval rearing laboratory of the British Museum (Natural History) during the past ten years and as a part of the ongoing studies on NE Atlantic brachyuran crabs. Specimens representing species (6) and (7) were collected during RRS *Discovery* Cruise 105 (1979) while the material of species (8) is from the collections of the *Michael Sars* North Atlantic Deep-Sea Expedition (1910).

Measurements: carapace length (cl) = distance between mid-line frontal and posterior margin of carapace; carapace width (cw) = distance from tip to tip of longest pair of antero-lateral spines.

Descriptions

(1) *Liocarcinus arcuatus* (Leach)

Portunus arcuatus, Lebour 1928: 510, Pl. VII, fig. 2 (1st–6th crab).

MATERIAL EXAMINED. Reared from ♀ collected at Kylesalia, Galway Bay, Ireland, 2.vii.1982, 1st crab–5 spms 1.5–1.7 mm cl., BM(NH) reg. no. 1983: 16, collid P. F. Clark.

Only the FIRST CRAB was obtained. Carapace (Fig. 1a) as long as broad; front slightly less than $\frac{1}{2}$ carapace width, median lobe small, deflected ventrally and obtuse; orbital dorsal margin forming a very broad even curve. Two prominent antero-lateral teeth; 1st not developed; 2nd represented as a minute, acute lobe; 3rd large, narrow, curved and acute; 4th not developed; 5th small, curved forward and acute.

Pereiopods 2–4 relatively thin; merus of 4th (Fig. 3a) length slightly exceeding $5 \times$ width, dactylus thin, styliform and straight throughout its length. Pereiopod 5 (Fig. 4a) dactylus narrow, length almost $5\frac{1}{2} \times$ maximum width.

(2) *Liocarcinus pusillus* (Leach)

Portunus puber, Williamson 1911: Pl. III, fig. 29; *Portunus pusillus*, Lebour 1928: 512, Pl. VII, fig. 1 (1st–6th crab).

MATERIAL EXAMINED: Reared from ♀ collected off Langness Point, Isle of Man, 23.vii.1975, 1st crab–5 spms 1.9–2.0 mm cl., BM(NH) reg. no. 1976: 249, coll'd A. A. Fincham. Deep Point, Scilly Isles, 33 m, 13.vii. 1964, 2nd crab–1 spm 2.3 mm cl., BM(NH) reg. no. 1968: 589; same locality, 14.vii.1966, 4th ? crab–1 spm 3.1 mm cl., BM(NH) reg. no. 1968: 475, coll'd BM(NH) and London University Sub-aqua Exped., Scilly Isles.

FIRST CRAB. Carapace (Fig. 1b) slightly longer than broad; front slightly less than $\frac{1}{2}$ carapace width, median lobe broadly rounded; orbital dorsal margin forming an angular curve. Two prominent, forwardly curved anterio-lateral teeth; 1st obtuse; 2nd represented as a minute, obtuse lobe; 3rd large, stout and acute; 4th forming a small sub-acute lobe; 5th large and acute.

Pereiopods 2–4 moderately stout; merus of 4th (Fig. 3b) length about $4\frac{3}{4} \times$ width, dactylus styliform and curved, noticeably shorter than merus. Pereiopod 5 (Fig. 4b), dactylus moderately broadened proximally, length about $4\frac{3}{4} \times$ maximum width.

LATER STAGES. Anterio-lateral teeth of carapace of 2nd crab similar to 1st stage. In 4th stage (Fig. 1c) all 5 teeth developed but 2nd and 4th less pronounced than others.

(3) *Liocarcinus depurator* (Linnaeus)

? *Portunus holsatus*, Williamson 1911: Pl. II, figs 13, 13a (1st crab); *Portunus depurator*, Björck 1913: 26, Taf. figs 5, 6 (1st crab); Lebour 1928: 515, Pl. VI, fig. 1 (1st–5th crab).

MATERIAL EXAMINED. Reared from ♀ collected in Strangford Lough, Co. Down, Ireland, 14.iv.1976, 1st crab–5 spms 2.1–2.5 mm cl., 2nd crab–5 spms 2.9–3.2 mm cl., BM(NH) reg. no. 1983: 17, coll'd A. A. Fincham.

FIRST CRAB. Carapace (Fig. 1d) broader than long; front less than $\frac{1}{2}$ carapace width, median and submedian lobes broad, inconspicuous and slightly emarginate; orbital dorsal margin strongly angular. Three prominent, forwardly curved anterio-lateral teeth; 1st broad and obtuse; 2nd represented as a small obtuse lobe; 3rd large, stout and acute; 4th small and acute; 5th large and acute.

Pereiopods 2–4 moderately stout; merus of 4th (Fig. 3b) length about $4\frac{1}{4} \times$ width, dactylus stout, terminally curved and almost as long as merus. Pereiopod 5 (Fig. 4c) dorsal margin of merus serrate, dactylus moderately broadened, length slightly exceeding $3\frac{1}{2} \times$ maximum width.

LATER STAGES. 2nd crab (Fig. 1e) with all 5 anterio-lateral teeth conspicuous; 2nd angular; 4th rather stouter than 5th, curved and acute.

(4) *Liocarcinus puber* (Linnaeus)

Portunus puber, Lebour 1928: 508, Pl. V, figs 3, 4 (1st–5th crab).

MATERIAL EXAMINED. Reared from ♀♀ collected from Lulworth Cove, Dorset, Sept. 1972, BM(NH) reg. no. 1974: 334, coll'd Guildford Sub-aqua Club and from near Plymouth, Devon, May 1973, coll'd Mar. Biol. Lab. Plymouth, 1st crab–5 spms 2.2–2.5 mm cl., 2nd crab–3 spms 3.0 mm cl., 3rd crab–5 spms 3.5–3.7 cl., 4th crab–1 spm 4.0 mm cl.

FIRST CRAB. Carapace (Fig. 1f) broader than long; front less than $\frac{1}{2}$ carapace width and faintly granular to denticulate, median lobe not developed; orbital dorsal margin forming a broad and regular curve. Three prominent anterio-lateral teeth; 1st large, stout and acute; 2nd represented by an obtuse lobe; 3rd stout, projecting outwards and acute; 4th just discernible as an obtuse projection; 5th small, stout, acute and projecting forward.

Pereiopods 2–4 moderately stout; merus of 4th (Fig. 3d) length almost $4 \times$ width, dactylus noticeably stout and styliform, slightly curved at apex. Pereiopod 5 (Fig. 4d), dactylus slightly broadened, length about $5 \times$ maximum width, terminally very acute.

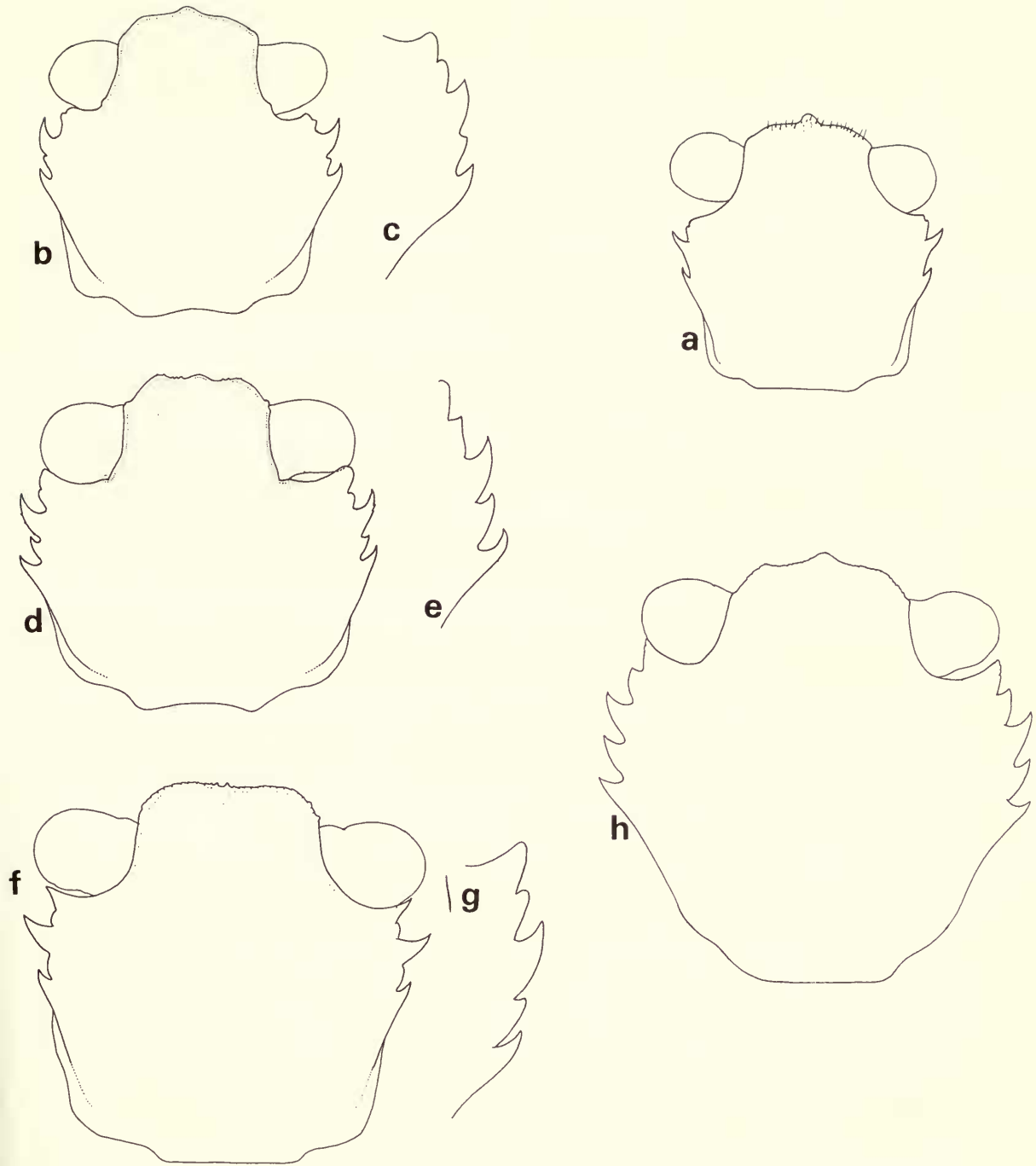


Fig. 1 a, b, d, f, h, outline dorsal aspects of carapace; c, e, g, antero-lateral teeth of right side: a, *Liocarcinus arcuatus*, 1st crab 1.7 mm cl; b, *L. pusillus*, 1st crab 1.9 mm cl; c, 4th crab 3.1 mm cl; d, *L. depurator*, 2.1 mm cl; e, 2nd crab 3.0 mm cl; f, *L. puber*, 1st crab 2.2 mm cl; g, 4th crab 4 mm cl; h *L. holsatus*, 1st crab 2.6 mm cl.

LATER STAGES. Anterio-lateral teeth of carapace of 2nd crab similar to 1st stage. In 4th stage (Fig. 1g) 2nd and 4th teeth prominent but obtuse.

(5) *Liocarcinus holsatus* (Fabricius)

Portunus holsatus, Lebour 1928: 514, Pl. VI, fig. 2 (1st–4th crab).

MATERIAL EXAMINED. Reared from ♀ collected in Port Erin region, Isle of Man, Feb. 1973, 1st crab–5 spms 2.8–3.1 mm cl., BM(NH) reg. no. 1974: 333, colld Mar. Biol. Lab. Port Erin. Same locality, Feb. 1979, 1st crab–5 spms 2.7 mm cl., BM(NH) reg. no. 1983: 19, colld J. Ellis and P. F. Clark.

FIRST CRAB. Carapace (Fig. 1h) almost as broad as long; front less than $\frac{1}{2}$ carapace width, median lobe prominent; orbital dorsal margin forming a more or less even curve, somewhat angular. Five prominent anterio-lateral teeth, all acute; 2nd smallest; 3rd largest; 5th directed outward.

Pereiopods 2–4 moderately stout; merus of 4th (Fig. 3e) margins serrate; length about $3\frac{3}{4} \times$ width, dactylus thin, styliform and evenly curved. Pereiopod 5 (Fig. 4e), merus about as long as propodus, dactylus moderately broadened, distally acute to subacute, length about $3\frac{1}{2} \times$ maximum width.

LATER STAGES. The anterio-lateral teeth of the 2nd crab stage are slightly more accentuated than in the 1st stage and from the 3rd stage resemble those of the adult form.

(6) *Macropipus tuberculatus* (Roux)

Larvae and post-larval stages unknown.

MATERIAL EXAMINED. *Discovery* stn 10113 #1, 10.ix.1979, 50°16.1'N: 13°31.6'W, 2755–2760 m, 4th ? crab–1 spm 5.1 mm cl., BM(NH) reg. no. 1983: 61. *Discovery* stn 10120 #1, 13.ix.1979, 49°27.5'N: 11°21.7'W, 400 m, 4th ? crab–230 spms 5.1–5.5 mm cl., 5th ? crab–25 spms 6.4–6.8 mm cl., 6th ? crab–5 spms 7.1–7.2 mm cl., BM(NH) reg. no. 1983: 15 & 1983: 63.

FOURTH ? CRAB. Carapace (Fig. 2a) broader than long; front less than $\frac{1}{2}$ carapace width, median and submedian lobes developed; orbital dorsal margin forming an even curve, a small incision present. Five prominent, forwardly curved anterio-lateral teeth; 1st, 3rd and 5th acute; 2nd and 4th smaller and subacute.

Pereiopods 2–4 thin; merus of 4th (not figured but see below under *later stages*) margins (and those of carpus) strongly serrate, dactylus styliform, thin and terminally curved, much longer than propodus. Pereiopod 5 (Fig. 5e) merus length about $3 \times$ width, dactylus moderately broadened, length slightly less than $4 \times$ maximum width and slightly longer than merus + ischium.

LATER STAGES. Specimens assigned here to the 5th and 6th crab stages do not differ significantly from the stage described above, except in having the anterio-lateral spines slightly more pronounced. Pereiopods 2–4 have the same proportions and armature as those attributed to the 4th crab stage. Pereiopod 4 of the 6th ? crab stage is shown in Fig. 5b and for comparison with that of the 6th ? stage of *Bathynectes longipes*; pereiopod 4 is missing from all available earlier stages of this latter species (see below). Pereiopod 4 moderately stout, meral margin serrate, length about $4 \times$ width, dactylus much longer than propodus.

(7) *Bathynectes longipes* (Risso)

Post larval stages unknown.

MATERIAL EXAMINED. *Discovery* stn 10110 #1, 7.ix.1979, 49°18.8'N: 11°42.8'W, 920–930 m, 5th ? crab–2 spms 5.3–5.6 mm cl., BM(NH) reg. no. 1983: 62. *Discovery* stn 10110 #5, 7.ix.1979, 49°17.0'N: 11°50.8'W, 935–1000 m, 5th ? crab–1 spm 5.2 mm cl., 6th ? crab–1 spm 6.9 mm cl., BM(NH) reg. no. 1983: 20. *Discovery* stn 10115 #15, 12.ix.1979, 49°45.4'N: 13°52.9'W, 10–100 m (sounding 3900–4000 m), 4th ? crab–1 spm 4.4 mm cl., BM(NH) reg. no. 1983: 14.

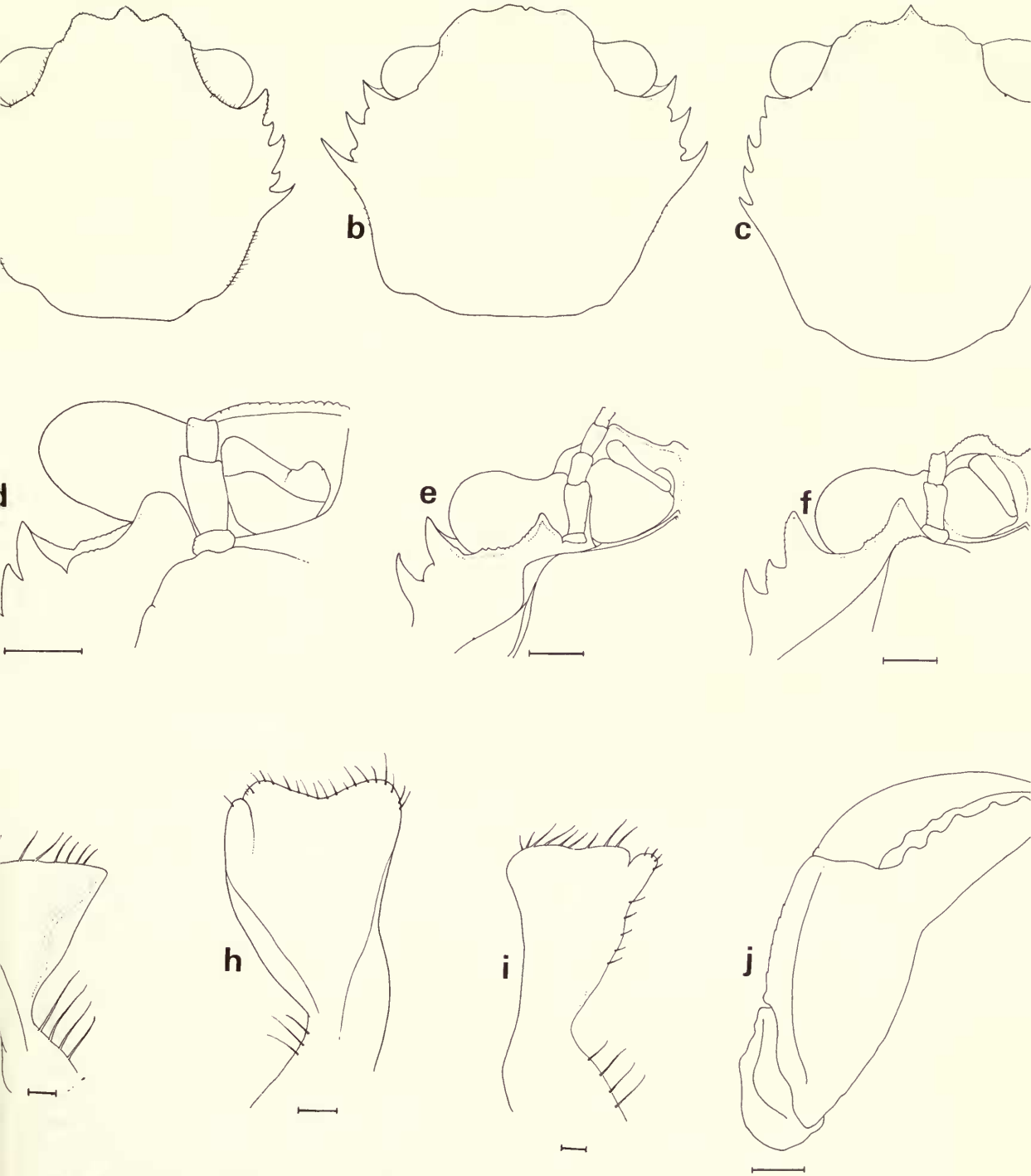


Fig. 2 Outline dorsal aspects of carapace: a, *Macropipus tuberculatus*, 4th ? crab 5.1 mm cl; b, *Bathynectes longipes*, 4th ? crab 4.4 mm cl; c, *Polybius henslowii*, 4th ? crab 4.4 mm cl. Ventral aspect of lower orbital margin: d, *L. puber*, 4th crab; e, *B. longipes*, 4th ? crab; f, *M. tuberculatus*, 5th ? crab (scale=0.5 mm). Distal part of endopod, 1st maxilliped: g, *P. henslowii*, 4th ? crab; h, *B. longipes*, 4th ? crab; i, *M. tuberculatus*, 5th ? crab (scale=0.1 mm); j, propodus and dactylus, right cheliped of *P. henslowii*, 4th ? crab (scale=0.5 mm).

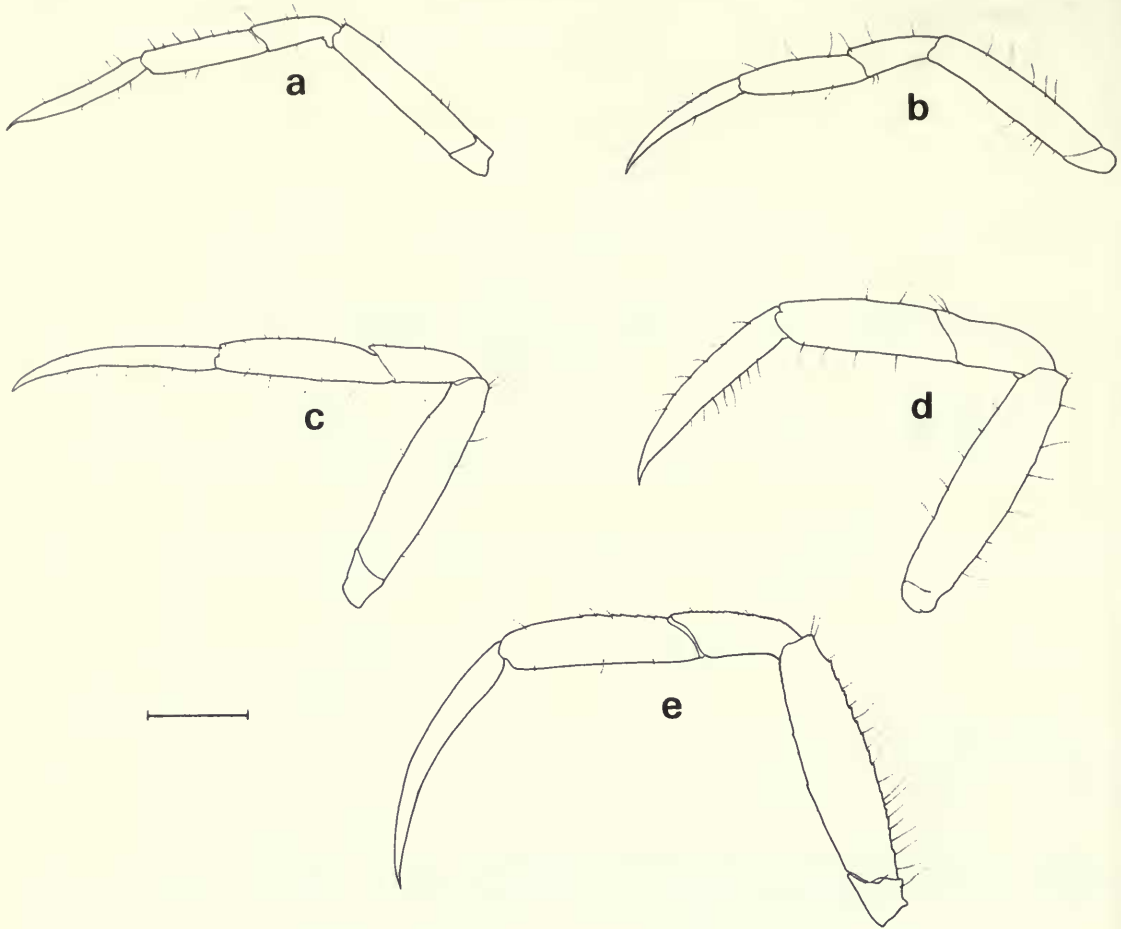


Fig. 3 Outline of 4th left pereiopod, 1st crab: a, *Liocarcinus arcuatus*; b, *L. pusillus*; c, *L. depurator*; d, *L. puber*; e, *L. holsatus* (scale=0.5 mm).

FOURTH ? CRAB. Carapace (Fig. 2b) broader than long, front less than $\frac{1}{2}$ carapace width, slightly sinuous, lobes not developed, a small median incision; orbital dorsal margin forming a somewhat angular curve and with a small incision. Three prominent, forwardly curved antero-lateral teeth; 1st, 3rd and 5th acute; 2nd and 4th represented as obtuse lobes; cervical groove moderately defined.

Pereiopods 2–3 thin (4th missing from all specimens of this stage examined, but see below under *later stages*). Pereiopod 5 (Fig. 5f) merus length about $2\frac{3}{4} \times$ width, dactylus moderately broadened, length about $4 \times$ maximum width and much longer than merus+ischium.

LATER STAGES. Specimens attributed here to the 5th stage differ only in size from the 4th stage described. The 4th pereiopod of a specimen assigned to the 6th crab stage is shown in Fig. 5c and for comparison with the same stage of *M. tuberculatus* (see Fig. 5b). Pereiopod thin, meral margin serrate, length slightly more than $5 \times$ width, dactylus longer than propodus.

(8) *Polybius henslowii* Leach

Polybius henslowii, Sivertsen & Holthius 1956: 49, fig. 32f (crab stages).

MATERIAL EXAMINED. *Michael Sars* stn 15, 22–23.iv.1910, 40°56'N: 9°28'W, 50 m, 4th ? crab–2 spms 4.4 & 4.5 mm cl., BM(NH) reg. no. 1983: 58; various stages–18 spms 4.8–10.2 mm cl., Bergen Museum.

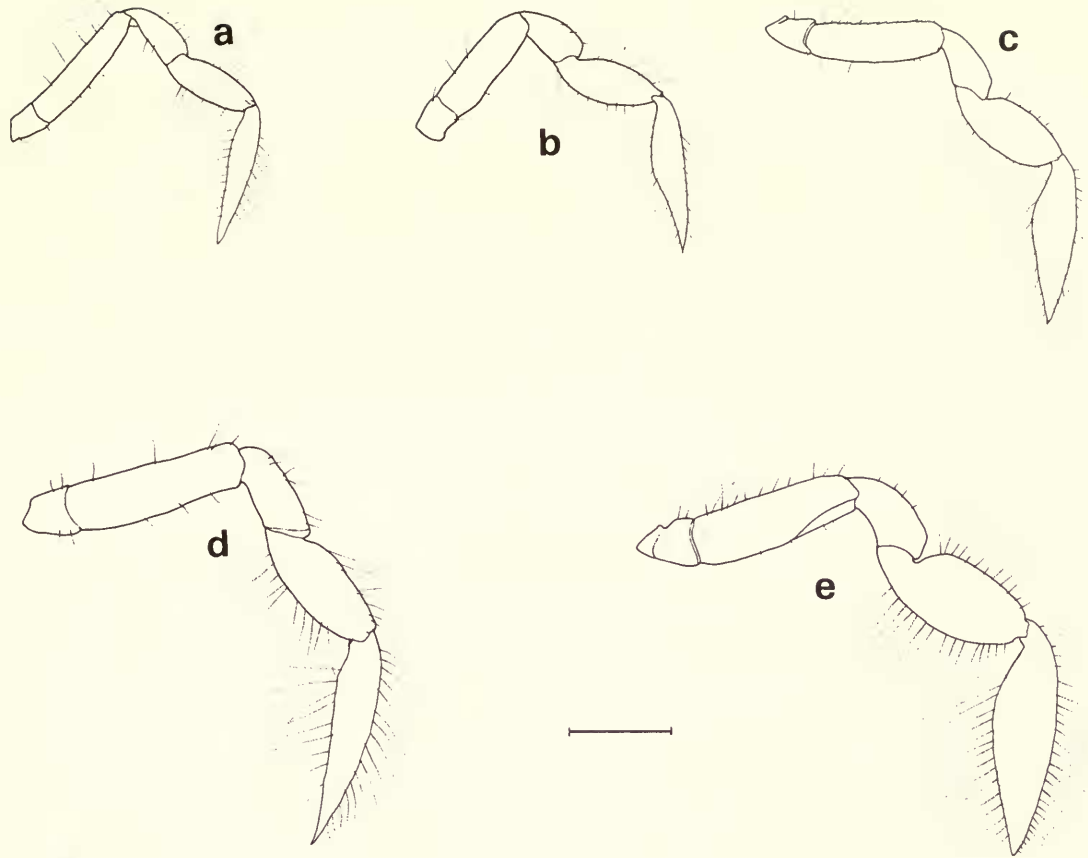


Fig. 4 Outline of 5th left pereiopod, 1st crab: a, *Liocarcinus arcuatus*; b, *L. pusillus*; c, *L. depurator*; d, *L. puber*; e, *L. holsatus* (scale=0.5 mm).

FOURTH ? CRAB. Carapace (Fig. 2c) slightly longer than broad; front less than $\frac{1}{2}$ carapace width, submedian lobes low and broad, median prominent and acute; orbital dorsal margin forming an even curve and with a small incision. Five prominent, forwardly curved anterio-lateral teeth; 2nd smallest and subacute; 3rd noticeably spinose. All pereiopods of these specimens are detached; the smallest, identifiable as the 4th and that of the 5th figured here, probably belong to the 5th and 6th crab stages respectively.

Pereiopods broad: merus of 4th (Fig. 5a) length slightly more than $3\times$ width, dactylus prominently lanceolate. Pereiopod 5 (Fig. 5d) dactylus broadened, length about $2\frac{1}{4}\times$ maximum width.

Remarks

Comparative studies of the first crab stages of the five laboratory reared *Liocarcinus* species have revealed two aspects of development. (1) that the species can be arranged in order of overall mean carapace sizes (see Table 1) showing a gradation from the smallest of 1.7 mm (*arcuatus*) to the largest of 2.7 mm (*holsatus*), and (2) that the first crab stage of *holsatus* is morphologically advanced compared with those of the other four species in that the full complement of anterio-lateral teeth are present and similar in shape to those of mature specimens. This definitive adult pattern of carapace teeth is not apparent in *arcuatus*, *pusillus*, *depurator* or *puber* until about the third or fourth crab stages (see Lebour 1928: Pl. V, fig. 4, Pl. VI, fig. 1, Pl. VII, figs 1-2).

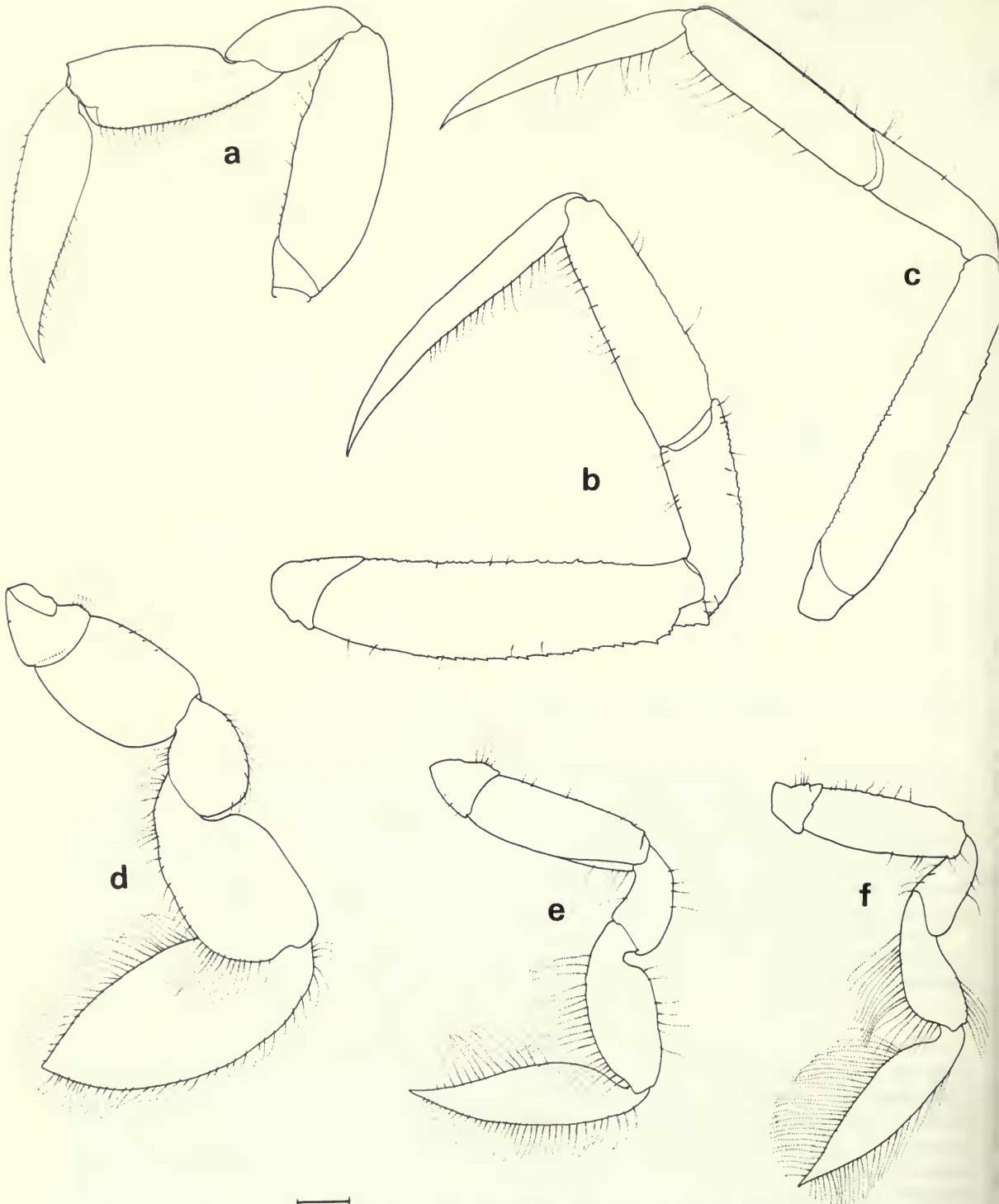


Fig. 5 Outline of 4th left pereiopod: a, *Polybius henslowii*, 5th ? crab; b, *Macropipus tuberculatus*, 6th ? crab; c, *Bathynectes longipes*, 6th ? crab. Outline of 5th pereiopod: d, *P. henslowii*, 6th ? crab; e, *M. tuberculatus*, 5th ? crab; f, *B. longipes*, 5th ? crab (scale=0.5 mm).

Table 1 Comparative carapace widths of first crab stages of five *Liocarcinus* species. (Mean values are given under PRESENT MATERIAL.)

	LEBOUR (1928)	PRESENT MATERIAL
<i>L. arcuatus</i>	1.6 mm	1.7 mm
<i>L. pusillus</i>	2.0 mm	1.8 mm
<i>L. depurator</i>	3.8 mm	2.2 mm
<i>L. puber</i>	2.8 mm	2.6 mm
<i>L. holsatus</i>	3.2 mm	2.7 mm

Lebour (1928) briefly described the early crab stages of all six species of *Liocarcinus*. The size ranges of her material were similar to those of the laboratory reared specimens of the five species reported here except for *L. depurator* (see below). There are a few apparent differences when our first crab stage material of *arcuatus*, *pusillus* and *depurator* is compared with Lebour's figures of this stage. The front of *arcuatus* is described by her as 'very slightly three-lobed, hairy', whereas our specimens have a small but distinct median lobe that is strongly deflected ventrally but hardly visible when the carapace is viewed dorsally.

The first crab stage of *L. depurator* figured by Lebour clearly shows all five antero-lateral teeth well developed; in our material this condition is not reached until the second stage (see Fig. 1e). This feature, and the large carapace size of Lebour's specimen (3.8 mm cw), suggest that her figure is of a second or third crab stage, although the first crab figured by Björck (1913) from plankton caught material measured 3.0 mm. Williamson (1915) figured the first crab stage (presumably obtained from a plankton caught megalopa) that he attributed to *Portunus holsatus*. This figure clearly shows conspicuous, slightly emarginate median and submedian lobes and has a carapace length of about 2.5 mm. These features, and the shape of the antero-lateral teeth are all characteristic of *depurator* and Williamson's specimen probably belongs to this species. Lebour (1928) also pointed out that the first crab assigned by Williamson to *Portunus puber* is probably an example of *pusillus*; the present study endorses this opinion.

The more advanced crab stages figured here of *Macropipus*, *Bathynectes* and *Polybius* have carapace lengths approaching those of the 4th–6th crab stages of laboratory reared *L. puber* and *depurator*; they have therefore been tentatively assigned to these respective stages. The carapace shape of juvenile *M. tuberculatus* differs from that of the adult, but it has been possible to identify these early crabs as *Macropipus* because the outer ventral orbital margin is without a v-shaped incision (see Fig. 2f) which is clearly present in *Liocarcinus* juveniles of a corresponding size (see Fig. 2d). This incision is also represented as a shallow notch in juveniles of *Bathynectes longipes* (see Fig. 2e).

The juveniles of *B. longipes* have been identified on the following combined features. (1) the narrow second segment of the antennal peduncle which does not fill the gap between the lower inner orbital margin and the frontal region; (2) the long slender pereopods (Fig. 5c); (3) the noticeable alternation in size of the antero-lateral teeth; (4) the undeveloped submedian and shallow median lobes of the front; (5) the moderately defined cervical groove. All these features are found in the adult *B. longipes*.

The carapace shape of juvenile crabs attributed to *Polybius henslowii* also differ from the adult form but these juveniles can be readily identified by the lanceolate dactyls of the 2nd–4th pereopods (Fig. 5a) and the distinctive shape of the cheliped (Fig. 2j); both are features of the adult crab. However, the juveniles of 4.4 mm cl. (4th ? crab) are without a lobe on the first maxilliped endopod (see Fig. 2g) which is prominent in adults of *P. henslowii* and is also developed in juveniles of a similar size of *M. tuberculatus* (see Fig. 2i), *Bathynectes longipes* (see Fig. 2h) and in corresponding stages of the *Liocarcinus* species examined.

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References

- Björck, W.** 1913. Biologische-Faunistische untersuchungen aus dem Oresund. *Lunds Universitets Årsskrift NF Afd. 2*, Bd 9 Nr 7: 1-39.
- Lebour, M. V.** 1928. The larval stages of the Plymouth Brachyura. *Proceedings of the Zoological Society of London*. Pt 2: 473-560.
- Rice, A. L.** 1980. Crab zoeal morphology and its bearing on the classification of the Brachyura. *Transactions of the Zoological Society of London* **35**: 271-424.
- Williamson, H. C.** 1911. Report on the larval and later stages of *Portunus holstatus*, Fabr., *Portunus puber*, L., *Portunus depurator*, Leach; *Hyas araneus* (L); *Eupagurus bernhardus*, L; *Galathea dispersa*, Spence Bate; *Crangon trispinosa* (Hailstone); *Cancer pagurus*, L. *Scientific Investigations of the Fishery Board for Scotland (1909)*: 1-20.

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